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ON THE OVULIFEROUS ORGAN OF *HIRMERELLA*

V. A. KRASSILOV

Institute of Biology and Pedology, Vladivostok, 22, U.S.S.R.

ABSTRACT

Mesozoic brachyphyllous plants which produced the *Classopollis*-type pollen grains have been conventionally assigned to the extinct family of conifers, Hirmerellaceae. It is shown that ovules in *Hirmerella* were enclosed in a cuticle-lined locule within the thick walled samaras. The double cuticle (locular + integumental) and nucelli are described in detail. The nucelli lack definite beaks or pollen chambers. These ovuliferous organs are compared with *Araucaria*, *Caytonia*, and *Leptostrobus*. It is suggested that *Hirmerella* and its allies stand apart from true conifers.

INTRODUCTION

Many Mesozoic plant assemblages were dominated by plants with brachyphyllous shoots bearing scale-leaves in spiral or decussate arrangement. Some of them have been assigned to Araucariaceae or Taxodiaceae. However many brachyphylls with convergently similar leaves seem to belong in extinct family or families. They produced peculiar pollen grains of *Classopollis* type which were ubiquitious in Mesozoic sediments but especially abundant in the near-shore marine facies suggesting coastal habitats. These pollen grains aroused much interest because of their angiosperm-like characters: collumellar layer (Pettit & Chaloner, 1964), subequatorial groove which might have performed a harmomegate function, as in *Nymphaea*, and a distal pore. Some palynologists have suggested gnetalean affinities for the *Classopollis*-producing plants (Srivastava, 1976). However the pollen-cones studied by Alvin *et al.* (1978) resemble those of *Araucaria* and some other conifers. The ovulate strobili, known as *Hirmer(i)ella* were also described as coniferous, though somewhat peculiar in having winged ovuliferous scales dispersed separately from the bracts (Jung, 1967). The ovules have not been adequately studied. Recently Harris (1979) was able to isolate two megaspore membranes enclosed in the samara (I prefer this noncommittal descriptive term to ovuliferous scale). He summarized the characters of the female structures as follows: " Female cones large and comprising many crowded scales, bract scale separate from ovuliferous scale; both scales robust and both ultimately falling from cone axis and normally separating. Bract scale simple, lanceolate. Ovuliferous scale with several terminal lobes which may overlap, lower part enclosing two seeds in epidermis-lined cavities " (Harris, 1979, p. 52).

I studied a few dispersed samara of *Hirmerella* collected by M. P. Doludenko during her visit to Poland. The samaras, together with many foliage shoots of *Pagiophyllum* type came from the brown clays near Odrovaz which contain also *Thaumatopteris shenkii*, *Phlebopteris angustifolia* and other index-species of the Hettangian stage. Comprehensive study of this flora is being undertaken by Dr. M. Reymanowna who generously helped in collecting the material.

RESULTS

Two incomplete samaras have been removed from the rock by hydrofluoric acid treatment. One of them shows two crescent-shaped wings and a narrow

pointed lobe between them (Plate 1, B). Another samara, 10 mm broad, has five overlapping wing lobes, clearly not in one plane (Plate 1, A). The lobes are triangular, straight or curved, bluntly pointed, of unequal width, resembling *Pagiophyllum* foliage leaves. The body and the lobes are strongly folded suggesting a bulky, nearly globose shape before flattening.

The five-lobed samara has yielded under maceration a thick outer cuticle, a double cuticle inside it, and two nucelli. The outer cuticle is of uniform thickness throughout the body and the lobes, with stomata more numerous on the lobes, arranged in rows corresponding to the macroscopically visible striation. The stomatal rows consist of thick-walled isodiametric cells, about 40 μm wide. The stomata are mostly oblique, occasionally longitudinal or transverse to the rows, amphicyclic, with normally a single complete ring of 5-6 encircling cells, but often with an incomplete second cycle of 2-3 cells. In more crowded stomata, some of the encircling cells are lacking, the neighbouring apparatuses contacting by subsidiary cells. Four to five petaliform subsidiary cells are considerably thickened. Stomatal pit is elliptical, 18 μm long. The guard cell thickenings, observed in SEM (Plate 1, D) are exceedingly small, attached by sagging poles, not forming T-shaped polar beams. The stomatal rows are separated by a few rows of elongate rectanguloid cells. The cells are papillate in both stomatal and interstomatal rows. *Classopollis* grains stick abundantly to the cuticle (Plate 1, C-D).

The outer cuticle is separated by a thick coaly layer from the double cuticle which is much thinner and shows a reticulate pattern of two intersecting cell rows (Plate 1, G). It is possible to disjoin fragments of the adnate cuticles by needle after alkali treatment. The outer layer, interpreted as the locule lining, shows the rows of elongate rectanguloid cells with somewhat oblique transverse walls. The longitudinal walls are either slightly undulate or definitely sinuous (Plate 1, F). The cell dimensions are variable: length 60-140 μm, width 15-25 mm, average 90×18 μm. Occasional cells are of double length as if they failed to divide. The inner layer, interpreted as the integument cuticle, shows the rows of elongate rectanguloid or fusiform cells, tapering to both ends, 60-72×15-18 μm with straight or bowed, strongly marked longitudinal walls.

The nucelli are easily separable from the enveloping cuticles, free to the base, pointing to the lobed margin of the samara, overlapping, diverging at acute angle (Plate 1, E). They are ovoid, 4 μm long, strongly folded by compression, broadly rounded at the chalazal end, tapered at the micropylar end, without a definite beak. One of the nucelli shows a triangular apical orifice (Plate 1, I). In the other nucellus, a short canal is discernible at the apex (Plate 1, H). Nucellar cuticle is moderately thick, showing irregular isodiametric cells about 100 μm wide. One of the nucelli contains a large megaspore.

No integumental cuticles were preserved between the nucelli. Conceivably, the integumental cuticles were thin at the contact of the ovules which had been pressed to each other.

DISCUSSION

My observations show that in this as in the Yorkshire species of *Hirmerella* the ovules were enclosed in a cuticle-lined locule, inside the thick-walled samaras. In the ripe samaras, the ovules were adpressed to the locule wall. The nucelli were free to the base, strongly cutinized. Lack of the definite nucellar beak and pollen chamber suggests, albeit indirectly, that pollen tubes developed outside the nucellus.

Morphologically the samaras of *Hirmerella* are rather fruits than ovuliferous scales. They are comparable in some respects with the fruits of *Caytonia* and *Leptostrobus*, also thick-walled, heavily cutinized, with abundant stomata, cuticle lined locule, ovules adpressed to the locule, integumental cuticles engaged in the double cuticle (in *Caytonia*) and free nucelli with vestigial beaks. These similarities may evidence common pteridospermous ancestry. Like *Leptostrobus*, the fruits of *Hirmerella* might consist of two ovuliferous scales joined by their margins. The lobes might have developed from sterile scales of the ovuliferous shoot, hence their leaf-like habit. Alternatively, the samaras might have been derived from the *Peltaspermum*-type cupule, the lobes of a cupule turning into the wing lobes. In any case it seems not easy to derive *Hirmerella* from conventional coniferous seed-scale complex.

Among the plants classified as conifers, *Araucaria* has similar "ovuliferous scales" enclosing one or occasionally two ovules. I studied samaras of several extant *Araucaria* species. My observations, to be published elsewhere, disagree with the customary interpretation of these structures. In *A. araucana*, the ovuliferous scales (or rather achenes) can be easily split open along the median suture. They reveal a locule lined with a thin cuticle. Nucellus is free to the base, covered with a moderately thick cuticle. This ovuliferous organ might have arised from the corresponding structures of *Hirmerella* or a common ancestor. Further consideration of phylogenetic relationships must await better understanding of *Hirmerella* and allied Mesozoic genera. With their unique pollen grains and ovuliferous structures they apparently stand apart from true conifers.

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EXPLANATION OF PLATE

PLATE 1

A. Compression of a samara showing overlapping lobes. × 5 (cuticular preparations are from this specimen). B. Incomplete samara with lobes of unequal width. × 5. C. *Classopollis* pollen grains on the papillate outer cuticle. × 500, SEM. D. Outer cuticle, inside view, showing small guard cell thickenings. × 600, SEM. E. Two overlapping nucelli, × 15. F. Cuticle lining the locule. × 170. G. Double cuticle showing intersecting files of the locular and integumental cells. × 170. H. Beak of a nucellus (the larger one) with vaguely discernible canal. × 500. I. Apical portion of the top nucellus showing small triangular orifice. × 500.